DETERMINATION OF DOMINANCE IN MENDELIAN INHERITANCE.

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The longer one investigates the phenomena of heredity the more one is impressed with the grandeur of the discovery made over forty years ago by Gregor Mendel. His method is not less important than its results. Following him, in studying heredity one considers a single character at a time. One notes the result in the offspring when this character assumes contrasted forms in the two parents or when one parent has the character and the other lacks it. Under these circumstances one frequently, nay, usually, finds that the condition in one parent dominates over that in the other parent, so that the offspring are all alike, and like one parent, in respect to that character. The opposite, or recessive, quality is not lost, however. It persists in the germ plasm and one half of the germ cells of the individuals belonging to the first generation of hybrids contain the dominant and one half the recessive quality.

Dominance, it will be observed, it a matter of the soma. The hybrid fertilized egg contains both contrasting qualities and so, probably, do all of the cells of the body. But only one of the qualities ordinarily makes its appearance. It has been suggested that a struggle occurs between the contrasted qualities and the stronger—called the *dominant*—wins. The question is what determines this assumed greater strength of the dominant quality? What determines dominance?

Various replies have been given to this question. It has been suggested that the dominant quality is the *older* and although this is sometimes true it so often fails to be so that age cannot be regarded as the primary cause of dominance. Frizzling and silkiness of fowl's feathers are each novelties but one dominates over the ordinary flat feather and the other is dominated by it. Much evi-

dence of this sort could be adduced proving the insufficiency of the theory of the recessive nature of novelties. A different theory has been suggested by deVries, namely, when an individual having the characteristic patent is crossed with one in which it is latent the patent characteristic is dominant, the latent recessive. A similar expression has been proposed by Hurst who concludes that the presence of a quality usually dominates over its absence. This expression of the facts is, in the main, true but it is too narrow, inasmuch as it assures that the mendelian result occurs only when a character is crossed with its absence; but this I shall show directly is by no means true.

Two years ago I suggested that a *progressive* variation, one which means a further stage in ontogeny, will dominate over a condition due to an abbreviation of the ontogenetic process—or a condition less highly developed than the first. Recent studies have thrown

a *b* *c* *d* *e*

FIG. 1.

additional light on this matter and I wish to treat it now generally. First let me present some illustrations. Many poultry have feathers on the feet; these constitute the so-called *boot*. If a "booted" bird be mated with a non-booted all offspring are booted—booting is dominant over its absence. Booting occurs, however, in an infinity of grades. For convenience I recognize ten, usually determined by inspection. If a bird with a boot of grade 8 or 9 be crossed with a bird with boot of grade 2 or 3, both being pure dominants, then the stronger condition is dominant in the offspring, so that their average grade is about 8.

A second illustration may be drawn from certain studies made on the asparagus beetle by Dr. F. E. Lutz, of the Carnegie Institution of Washington. In the embryonic condition the outer wing covers of this beetle are nearly pigmentless or yellow. Before

emerging from the pupal condition black pigment is laid down. The pigmented area is variable in amount. The more extensively pigmented condition is dominant over the less extensively pigmented (*a* over *c, d* or *e*—see Fig. 1). In this case, also, it is clear that the facts are better expressed by the statement that the more developed condition dominates over the less developed.

Still another case is that of human eye color. The pigmentation of the iris is variable in amount. The blue iris is without pigment. A small amount of black pigment (with or without yellow) produces the grays; still more pigment yields browns and blacks. Now it appears that the offspring of parents one of whom has gray eyes and the other blue eyes will have gray eyes or blue eyes, but not brown eyes; and gray will show itself dominant over blue. Similarly brown iris color is dominant over gray; the more advanced condition of pigmentation over the less advanced. We have not here to do with a qualitative difference of the presence of a character opposed to its absence, but of a qualitative difference only.

The heredity of human hair color follows a similar law. In one series red pigment is absent in the hair and such colors as flaxen or tow, light brown, brown, dark brown and black may be distinguished. The records collected by Mrs. Davenport and myself show that two flaxen-haired parents have flaxen-haired children and probably only such. Two parents with light brown hair have chilapparently only such. Two parents with light brown hair have children of two parents each with dark brown or black hair produce children with all of the varieties of hair color. This result means that any lighter color is recessive to any darker color.

The facts recited above and many others thus support the view that, where various stages, *a, b, c,* in the progressive development of a quality are found in individuals of the same race or species, the more progressive condition will often behave as a dominant toward the less progressive condition. The extreme case is, of course, that in which the organ or quality is absent in one parent and present in the other; but this seems to be only a special case of a more general law.

As to the universality of this law it is still early to speak with confidence. We know too little of the developmental factors of an

organ to decide, in many cases, whether a difference is due to a progressive or a retrogressive change. For instance, the long angora coat of rabbits is recessive to short coat; and this has been cited as a clear case of recessiveness of the advanced condition. But it seems doubtful if such is the case. For the angora coat retains an embryonic quality (viz., of continued growth) which is present in the infancy of the short-haired rabbit and is then inhibited. The inhibiting factor is present in short-haired rabbits and absent in angora rabbits and the presence of the inhibiting factor dominates over its absence. At one time I thought that the dominant white plumage of some poultry was a case of dominance of absence of color. But it now appears that we have among poultry recessive whites which are true albinos, and the *dominant* whites which must be regarded as "grays," in which pigmentation is obscured by an additional factor like that which turns black hair gray. This graying factor is dominant over its absence.

It is possible that the future may show that, in accordance with the ideas of deVries, an advanced grade of a character may be regarded as a sum of minute equivalent elementary units; by the dropping out of these units one at a time a character passes through a series of degradational stages. Then a light brown hair may have one unit of melanic pigment, brown hair two units, dark brown three units, and black hair four units. If this should prove to be true then the four unit condition would dominate over the three unit condition, or the fourth unit would dominate over its absence. But such evidence as I have at present does not favor this view. I am inclined rather to the hypothesis that when the germinal determiner of greater intensity meets that of less intensity it dominates over the latter. This hypothesis receives support from another set of facts which go to prove that the idea of varying intensity of a determiner is a true one. This set of facts is derived from the combs of poultry. In one race of poultry—Polish fowl—the comb consists of a pair of horns or broad flaps which lie far back near the base of the beak; and there is no median comb. In the Minorca and most other fowl there is a single median comb. Now when these two races are crossed we find that the median comb dominates over the absence of median comb; sometimes *completely,* running in the

hybrid from the base of the beak to in front of the nostrils; sometimes *incompletely,* occupying only the anterior half or fourth of the beak. It seems to me clear that in the varying proportions of this median comb in the hybrids we have at once evidence for, and a measure of, varying intensity of dominance. Now it may reasonably be asked whether, when the long-combed and short-combed hybrids are mated together, the long comb dominates over the short. The answer is complicated by the fact that the Polish "horns" reappear in this second generation; but, leaving this aside, we find that there is a greater preponderance of *long* median combs than simple mendelian expectation calls for and this indicates that the longer median comb tends, but not always perfectly, to dominate the shorter median comb; or, in other words, the more intense determiner dominates the less intense.

To sum up, I think it is clear that dominance in heredity appears when a stronger determiner meets a weaker determiner in the germ. The extreme case is that in which the strong determiner meets a determiner so weak as to be practically absent as when a red flower is crossed with a white. In such cases we have the clearest examples of mendelian inheritance. But there is an entire gamut of cases where the opposed determiners are of varying relative potency. The phenomenon of determinance is seen in these cases also; but the mendelian law in them is sometimes obscured and sometimes merely not applicable.

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